Soybean Aphid Population Dynamics, Soybean Yield Loss, and Development of Stage-Specific Economic Injury Levels

Michael A. Catangui, Eric A. Beckendorf, and Walter E. Riedell*

ABSTRACT

Stage-specific economic injury levels (EILs) form the basis of integrated pest management for soybean aphid (*Aphis glycines* Matsumura) in soybean [*Glycine max* (L.) Merr.]. Experimental objectives were to develop a procedure for calculating EILs of the soybean aphid specific to the R2 (full bloom), R4 (full pod), and R5 (beginning seed) soybean development stages using the law of the diminishing increment regression model. Soybean aphid population growth over time appeared to follow the symmetrical bell-shaped and logistic growth curve models. Peak soybean aphid population levels and rates of increase occurred at the R5 development stage and then declined sharply thereafter. Highest peak soybean aphid populations were 21,626 aphids plant^{-1} for infestations starting at V5, and 6446 aphids plant^{-1} for infestations starting at R2. Highest maximum aphid-days plant^{-1} recorded were 537,217 for V5-introduced soybean aphids and 148,609 aphid-days plant^{-1} for R2-introduced soybean aphids. On average, the calculated maximum possible yield loss was 75% for soybean aphid infestations starting at the V5 (five node) stage and 48% for soybean aphid infestations starting at the R2 stage. Interrelationships among the current or predicted market value of soybean, cost of soybean aphid control, and the yield potential of the soybean field were considered in the calculations of the stage-specific EILs. Practical examples for calculating stage-specific EILs are presented. Economic injury levels were calculated both as soybean aphids plant^{-1} and soybean aphid-days plant^{-1}. Use of these stage-specific EILs may enable growers to manage soybean aphids more accurately.

THE SOYBEAN APHID is perhaps the most injurious insect pest of soybean in several regions of the United States. Soybean aphids can severely reduce crop biomass, soybean yield, and seed oil content (Beckendorf et al., 2008). Recent studies indicate that soybean aphids can adversely impact critical plant physiological processes associated with soybean yield and seed composition. Soybean aphid feeding injury can reduce soybean photosynthetic rates by up to 50% in infested leaflets. Feeding injury affects biochemical pathways for restoring chlorophyll to a low energy, light-receptive stage (Macedo et al., 2003). Riedell et al. (2009) presented evidence that soybean aphids are capable of reducing total nodule volume plant^{-1} by 34%, nodule leghemoglobin content by 31%, plant nitrogen fixation rate by 80%, and shoot ureide-N concentration by 20%.

Soybean aphids have very high reproductive potential. A single soybean aphid, for example, introduced on soybean at V5 can multiply to about 4000 plant^{-1} and reduce seed yield by 38% (Beckendorf et al., 2008). Ragsdale et al. (2007) estimated the soybean aphid doubling time to be between 2.7 and 13.4 d. Thus, an soybean aphid population of 200 soybean aphids plant^{-1} can exceed an EIL of 700 soybean aphids plant^{-1} within 6 d in some areas of the midwestern United States during a typical growing season, leaving soybean growers unprepared to effectively manage soybean aphids.

Essential to the integrated pest management of the soybean aphid is the availability of a practical decision making tool that considers the interrelationships among soybean yield, market value, and the cost of controlling the insect pest. We advance in this paper the development of a stage-specific decision-making tool that considers soybean plant developmental stages, timing of soybean aphid infestation, soybean aphid population dynamics in relation to soybean developmental stages, soybean yield potential, soybean market value, and cost of controlling the soybean aphid. Parameters were quantified using well-established biological models such as "the law of the diminishing increment" model (Spillman, 1924) to describe the quantitative relationship between soybean aphid numbers and yield loss, and the symmetrical bell-shaped and logistic growth models (Sit and Poulin-Costello, 1994) to describe the development of soybean aphids over time. Stage-specific EILs may enable growers to manage soybean aphids more accurately by considering in their decision-making the current or predicted soybean crop market value, soybean aphid control costs, and yield potential of their soybean field. Also, stage-specific EILs may give growers enough lead time to choose at which plant developmental stage they wish to control the soybean aphid pest during the growing season. Experimental objectives were to develop a procedure for calculating EILs of the soybean

M.A. Catangui, Plant Science Dep., South Dakota State Univ., Brookings, SD 57007; E.A. Beckendorf and W.E. Riedell, USDA-ARS, North Central Agricultural Research Lab., Brookings, SD 57006. Received 18 Dec. 2008. *Corresponding author (walter.riedell@ars.usda.gov).

Abbreviations: ADEIL, cumulative aphid-day economic injury level; DOY, day of year; EIL, economic injury level; GT, gain threshold; GTP, gain threshold expressed as proportion of the yield potential; R stage, reproductive stage; V stage, vegetative stage.

aphid specific to the R2 (full bloom), R4 (full pod), and R5 (beginning seed) soybean development stages using the law of the diminishing increment regression model.

MATERIALS AND METHODS
Soybean Field Conditions

Procedures followed in this study were similar to those described by Beckendorf et al. (2008) and Beckendorf (2005). Field studies were conducted in 2003 and 2004 on a Barnes clay loam soil (fine-loamy, mixed, superactive, frigid Calcic Hapludolls) at the Eastern South Dakota Soil and Water Research Farm near Brookings, SD. The plots used in this experiment were planted with winter wheat in the previous season. The 0.2 ha experimental site was tilled using a chisel plow in the fall and a disk-harrow in the spring for seedbed preparation. Pioneer 91B91 Roundup Ready soybean seeds (Pioneer Hi-Bred International, Inc., Johnston, IA) were planted on 22 May 2003 and 27 May 2004 using a John Deere 7200 Max-Emerge 2 (Deere & Company, Moline, IL) planter. The seeds were inoculated with *Bradyrhizobium japonicum* (Kirchner) (Nitragin, Milwaukee, WI) before planting. Planting depth was 4 cm and the seeding rate was 558,000 seeds ha^{-1}. Rows were 72 cm apart and planted in an east–west direction. Fertilizer was applied in a band 5 cm deep and 5 cm to the side of seed furrow at a rate of 16.8 kg ha^{-1} N, 43.8 kg ha^{-1} P$_2$O$_5$, and 15.6 kg ha^{-1} K$_2$O. Herbicides (alachlor and glyphosate) were applied at planting to manage weeds.

Soybean Aphid Field Cages

Soybean experimental plots to be infested with soybean aphids were enclosed in cages at the V2 (second node; Ritchie et al., 1999) developmental stage on 27 June 2003 and 28 June 2004. Each cage, which measured 1.5 by 1.5 by 1.5 m, was centered on two rows of soybean plants. Cages were used to keep other soybean pests (bean leaf beetles, grasshoppers, potato leafhoppers, and soybean leaf miners) from feeding on the soybean plants and potentially confounding the response variables being measured. The screening material was an amber-colored Lumite screen (18 × 14 mesh in^{-1}; BioQuip, Gardena, CA). Amber-colored Lumite screening is commonly used in field research and is known for good sunlight penetration and low air resistance (Bell and Baker, 2000; Lefko et al., 2000).

Each cage was equipped with a zippered opening that was located on the west end of the cage. The screening was fastened onto the frame using plastic ties, and the cage frame itself anchored to the soil using concrete reinforcing bars. Plant stands within each cage were thinned by hand to 30 soybean plants for each of the two rows enclosed in the cage (60 plants cage^{-1}). Color coded plastic ties loosely placed around the base of randomly chosen plants indicated when and which plants were to be removed for soybean aphid counts or yield data. A total of 32 experimental plots were enclosed in cages during the 2003 growing season, while 48 were enclosed during 2004.

Soybean Aphid Infestation

During the growing season, soybean plants were infested with known numbers of soybean aphids at the V5 (fifth node) and R2 (full bloom) soybean developmental stages (Ritchie et al., 1999). The V5 infestations were accomplished on 7 July 2003 and 12 July 2004, and R2 infestations were accomplished on 23 July 2003 and 27 July 2004. Initial infestation levels for both V5 and R2 soybean plants during the 2003 growing season were 0, 10, 50, and 100 soybean aphids plant^{-1}. In 2004, the initial infestation levels were 0, 1, 3, 10, 50, and 100 soybean aphids plant^{-1}. The treatments were assigned to cages as a completely randomized experimental design (Gomez and Gomez, 1984). Each initial soybean aphid population treatment per infestation period was replicated four times.

Soybean aphids used for infestation were produced at the rearing facility at the North Central Agricultural Research Laboratory in Brookings, SD. The soybean aphids used in this research were clones of wild soybean aphids collected from commercial soybean fields. The colony was maintained on Pioneer 91B01 soybean (Pioneer Hi-Bred International, Inc., Johnston, IA) inside environmental chambers (Conviron, CMP4030, Winnipeg, Canada) at 24°C and photoperiod of 16:8 (light–dark). Leaves from infested laboratory-reared plants were collected; wingless soybean aphids (varying in age) were counted and leaves were cut into pieces that contained the desired number of soybean aphids. The cut leaves containing the soybean aphids were then placed in a 240-mL foam cup and covered with a lid. Cups filled with the desired treatment populations were taken to the corresponding treatment cage in the field, and the leaf pieces containing known numbers of soybean aphids were carefully placed on the uppermost growing point of each soybean plant. These known initial soybean aphid populations were then allowed to establish on the plant and multiply freely. Check (0 soybean aphid plant^{-1}) cages were kept soybean aphid-free by applying insecticides [(0.02% pyrethins plus 0.20% piperonyl butoxide (Schultz Plant Spray, Expert Gardener Houseplants and Gardens, Bridgeton, MO) in 2003; and 0.425% esfenvalerate (Ortho Bug B Gone Multi-purpose Insect Killer, The Scotts Miracle-Gro Company, Marysville, OH) in 2004].

Soybean Aphid Population Measurement

Soybean plants that were to be sampled for soybean aphids at specific dates were randomly tagged using color-coded plastic ties at the time the cages were set on the field. Plants were sampled starting 3 d after initial soybean aphid infestation at the V5 soybean development stage or 2 d after soybean aphid infestation at the R2 soybean development stage, followed by sampling once every two weeks. Plant shoots were severed at ground level, placed in 49-L plastic bags, and stored in a freezer. Whole-plant soybean aphid populations were then counted using a magnifying lens and tally counter. Average soybean aphid populations for two plants removed from each cage were used for statistical analyses.

Population dynamics over time of each initial soybean aphid treatment was determined by fitting a symmetrical bell-shaped curve to the data through nonlinear regression analysis (PROC NLIN; SAS Institute, 1989). The mathematical equation fitted to the day of year (DOY) (X) and soybean aphid number plant^{-1} (Y) data was:

$$Y = A[B^{(X-C)^2}]$$

where A is the peak soybean aphid number plant^{-1}, B is a constant, and C is the DOY when the peak soybean aphid number plant^{-1} occurred.

Soybean aphid-days plant^{-1} and cumulative soybean aphid-days plant^{-1} were calculated according to Ruppel (1983), Kieckhefer et al. (1995), and Beckendorf et al. (2008). The pattern and rate of soybean aphid-day accumulation over time were determined by fitting a logistic curve to the DOY and cumulative soybean aphid-days plant^{-1} data for each treatment through nonlinear regression analysis (PROC NLIN; SAS Institute, 1989). The logistic equation fitted to the DOY (X) and cumulative soybean aphid-day plant^{-1} (Y) data was:

$$Y = A/[1 + e^{(B - CX)}]$$

where A is the maximum cumulative soybean aphid-day plant^{-1}, e is the base of natural logarithms, and B and C are constants. The quotient of B and C estimated the inflection point (Sit and Poulin-Costello, 1994; Dybing et al., 1988) or the DOY when the soybean aphid numbers were multiplying the fastest during the growing season. The DOY corresponding to the end of the lag phase of the logistic curve was estimated as $(B – 2)/C$ while the end of the log phase was estimated as $(B + 2)/C$ (Dybing et al., 1988). The lag phase is the time when the soybean aphids are reproducing the slowest while the log phase refers to the time when the soybean aphids are multiplying logarithmically.

Impact of Soybean Aphids on Soybean Yield

At the end of the growing season (29 Sept. 2003 and 6 Oct. 2004), seeds from all plants cage^{-1} were harvested by hand. Seed moisture was measured with a whole grain analyzer (DICKEY-john Co., Auburn, IL). Seed yields were expressed on a 10 g kg^{-1} moisture basis. Plot seed yields were expressed both in kg ha^{-1} and as proportions (%) relative to the highest or maximum plot yield recorded per growing season.

The relationship between seed yields and soybean aphid numbers at specific soybean growth stages was determined by fitting a power curve through nonlinear regression analysis (PROC NLIN; SAS Institute, 1989). The power equation fitted to the soybean aphid numbers (X) and seed yield (Y) data was:

$$Y = A(X + 1)^{-B}$$

where A and B are constants. The same equation also was fitted to the soybean aphid numbers (X) and proportion of maximum yield (Y) data. The coefficient of determination for each regression equation (R^2) was calculated as $R^2 = 1 –$ (residual sum of squares/corrected total sum of squares) (Kvalseth, 1985) (PROC NLIN; SAS Institute, 1989).

Yield Loss and Calculation of Stage-Specific Economic Injury Levels

Percentage yield loss was calculated as $(1 –$ yield as proportion of the maximum yield$) \times 100$. The soybean aphid numbers observed at specific soybean plant stages (R2, R4, and R5) were regressed against percentage yield loss. Three separate regression equations were developed for calculating stage-specific

EILs for the soybean plants initially infested with soybean aphids at V5 and R2.

A negative exponential curve widely used in agronomic research (other names: the law of the diminishing increment, law of diminishing returns, law of the soil, law of physiological relations [Spillman, 1924], Mitscherlich's regression law [Gomes, 1953], Mitscherlich response [Mead, 1988], asymptotic regression [Bliss, 1970]) was fitted to the soybean aphid number–percentage yield loss data set using the Marquardt's nonlinear regression algorithm (PROC NLIN, SAS Institute, 1989). The Mitscherlich regression was first applied in pest management by Catangui et al. (1997) to calculate the EILs of stable flies on feeder heifers in Nebraska.

The Mitscherlich regression equation describing the mathematical relationship between soybean aphid number (X) and percentage yield loss (Y) was:

$$Y = A(1 – e^{-BX})$$

where A is the upper asymptote and e^{-B} is the ratio between any two consecutive increments in yield loss due to two consecutive unit increments in soybean aphid number (Spillman, 1924). The coefficient of determination for each regression equation (R^2) was calculated as:

$$R^2 = 1 – \text{(residual sum of squares/corrected total sum of squares)}$$

(Kvalseth 1985) (PROC NLIN; SAS Institute 1989). The 2003 and 2004 soybean aphid number–percentage yield loss data sets were combined per initial date of soybean aphid infestation (V5 or R2). This was accomplished after F tests for homogeneity of error variances of the soybean yields indicated homogeneous error variances in the V5 and R2 infestation treatments (calculated $F <$ tabular $F_{0.01} = 99.5$, df = 2, 4) (Gomez and Gomez 1984). The Mitscherlich regression equation was then fitted to the combined 2003 and 2004 soybean aphid numbers and percentage yield loss data using the same methodology described above. Estimates of A (a) and B (b) were then used to calculate the EIL of soybean aphids as follows:

$$GTP = a[1 – e^{-b(\text{EIL})}]$$

or in logarithmic form,

$$\text{EIL} = \{\ln[1 – (\text{GTP}/a)]\}/–b$$

where EIL is the estimated EIL of the soybean aphids on soybeans, GTP is the gain threshold (GT) expressed as a proportion of the yield potential of the field, a is the theoretical maximum possible yield loss that soybean aphids can inflict on the soybean plant, and b is an estimate of the ratio between any two consecutive increments in yield loss due to two successive unit increments in soybean aphid number. Gain threshold is the control cost divided by the market value (Stone and Pedigo, 1972). In this paper, GT was equivalent to the soybean yield that will pay for the cost of controlling soybean aphids on the field. The soybean aphid infestation level that reduced soybean yield by the same magnitude as the GT was the EIL. A similar

procedure that allowed for calculating soybean aphid EILs in terms of cumulative soybean aphid-days plant^{-1} was also developed.

The three steps for calculating the EIL of soybean aphids on soybean were: (i) Calculate the GT:

$$GT\ (kg\ ha^{-1}) = control\ cost\ (\$/ha)/$$
$$soybean\ market\ value\ (\$/kg),$$

(ii) express the GT as a percentage of the soybean yield potential of the field (GTP), and (iii) calculate the EIL (number of soybean aphids per plant or number of soybean aphid-days per plant) using the logarithmic form of the negative exponential regression formula.

Weather Data

Weather data were obtained from an automated weather station maintained by the South Dakota State University Agriculture and Biosystems Engineering Department located 3.2 km south and 1.6 km east of the research plots. Cumulative growing degree days (GDD) (4.4°C lower limit, 30°C upper limit) were calculated as soon as the soybean aphids were introduced on the field. A GDD unit was calculated as GDD = [(highest daily air temperature ≤ 30°C + lowest daily air temperature ≥ 4.4°C)/2] – 4.4°C.

RESULTS AND DISCUSSION
Soybean Aphid Population Dynamics

The symmetrical bell-shaped curve appeared to perfectly fit the DOY-soybean aphid plant^{-1} data (Fig. 1A–1D, and 2A–2E). The regression equation enabled us to estimate the peak number of soybean aphids attained plant^{-1}, the DOY when peak soybean aphid numbers occurred during the growing season, and the number of days it took to reach peak soybean aphid numbers. The highest peak soybean aphid number attained in 2003 was 21,024 soybean aphids plant^{-1}, recorded in plants initially infested with 10 soybean aphids plant^{-1} at the V5 stage (DOY 188; 7 July) (Fig. 1B). This peak soybean aphid number was attained at R5 on DOY 231 (18 August), 43 d after soybean aphid introduction to the host plants. Cumulative GDD at the time of peak was about 766°C. Higher initial infestation rates of 50 and 100 soybean aphids plant^{-1} at V5 did not necessarily result in proportionately higher peak numbers. Peaks attained from these higher initial treatments were in fact lower at about 15,430 and 10,736 soybean aphids plant^{-1} (Fig. 1C–1D). Initial infestation rates of 10, 50, and 100 soybean aphids plant^{-1} required 40–43 d to reach their peaks near the R5 plant stage. Low levels of soybean aphids were detected in some of the control plots (Fig. 1A) perhaps because of soybean aphids being accidentally introduced during initial field setup. These unplanned low soybean aphid numbers added serendipitous data in 2003 because the lowest planned initial infestation of 10 soybean aphids plant^{-1} still resulted in very high soybean aphid numbers later in the season. Peak soybean aphid number in this serendipitous soybean aphid infestation occurred at R4 stage, 31 d after infestation (Fig. 1A).

In 2004, increasing initial soybean aphid numbers of 1, 3, 10, and 50 soybean aphids plant^{-1} introduced at V5 on DOY 194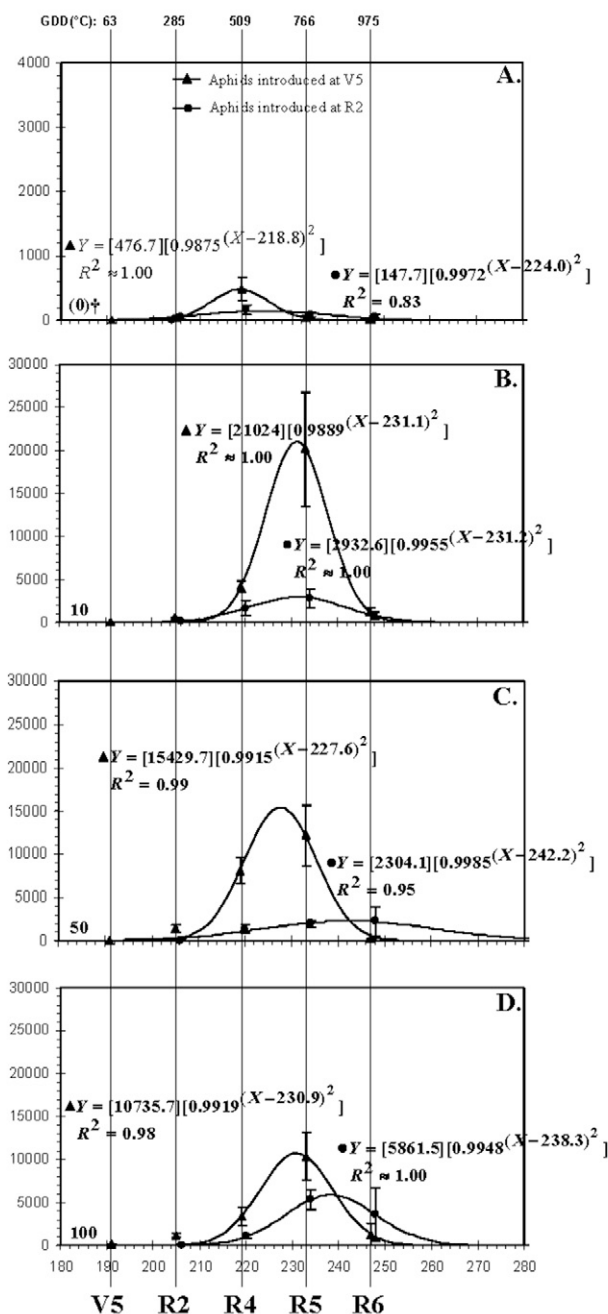 (12 July 2004) resulted in increasing peak soybean aphid numbers of 3486, 8924, 14,118, and 21,626 soybean aphids plant^{-1} (Fig. 2A–2D). The highest peak population attained, 21,626 soybean aphids plant^{-1}, occurred on DOY 237 (24 Aug. 2004), close to the R5 stage, around 650°C cumulative GDD, and 43 d after initial infestation, with 50 soybean aphids plant^{-1} at V5 (Fig. 2D). Initial infestation of 100 soybean aphids plant^{-1} did not result in further increase in peak soybean aphid number (Fig. 2E). Initial soybean aphid numbers introduced at V5 influenced the time of peak occurrence. Higher initial infestation numbers peaked earlier than lower initial infestation numbers (Fig. 2A–2E). For example, peak soybean aphid number occurred 58 d after infestation (at R6) in plants initially infested with 1 soybean aphid plant^{-1} at V5 (Fig. 2A). In contrast, peak occurrence was 20 d earlier (between R4 and R5) in plants initially infested with 100 soybean aphids plant^{-1} (Fig. 2D). Initial infestation levels of 10 and 50 soybean aphids plant^{-1} reached their peaks at about the same time near R5, 43 to 44 d after initial infestation (Fig. 2C–2D).

There were marked differences in the peak soybean aphid numbers each season, time of peak occurrence, and the number of days required to reach peak between plants initially infested at V5 and R2 (Fig. 1A–1D, and 2A–2E). In general, peaks were lower on the soybean plants infested at R2 than at V5. Peak soybean aphid numbers in the R2-infested soybean were 45 to 86% lower than V5-infested soybean in 2003, and 51–79% lower in 2004. R2-introduced soybean aphids also peaked later in the season than V5-introduced soybean aphids by 0 to 14 d in 2003 and 3 to 10 d in 2004. The R2-introduced soybean aphids required 21 to 24% fewer days to reach peak numbers than the V5-introduced soybean aphids. The R2-introduced soybean aphids took 2 to 16 fewer days to peak than V5-introduced soybean aphids in 2003, and 5 to 18 fewer days in 2004.
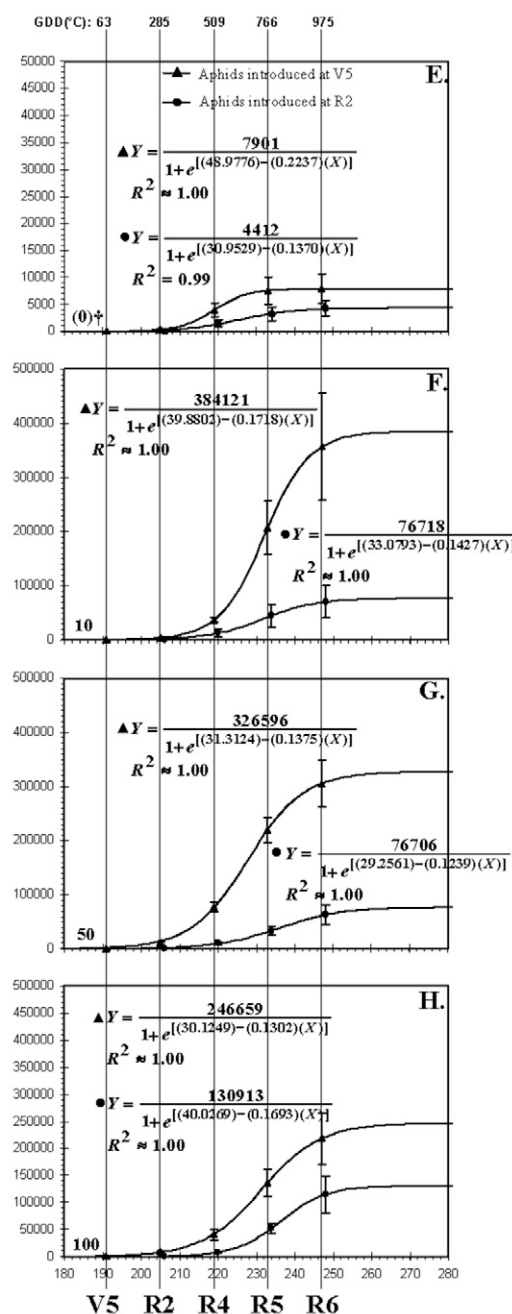
The logistic curve perfectly fitted the DOY-cumulative soybean aphid-day plant^{-1} data (Fig. 1E–1H, Fig. 2F–2J). Soybean aphid-day unitage (one soybean aphid feeding on one plant for a 24-h period) measures the combined intensity and duration of the soybean aphids on the soybean plants (Kieckhefer et al., 1995; Ruppel, 1983). Soybean aphid-day values are obtained by multiplying soybean aphid population numbers by the number of days that the soybean aphids were on the host plant. The inflection point of the logistic curve in this study represents the time during the growing season when soybean aphid-days were accumulating the fastest on the soybean plant. The upper asymptote of the logistic curve represents the maximum possible cumulative soybean aphid-days plant^{-1}, or the maximum severity inflicted by the soybean aphids to the soybean plants, during the growing season.

In 2003, an initial infestation of 10 soybean aphids plant^{-1} at V5 on DOY 188 (7 July) resulted in 384,121 maximum cumulative soybean aphid-days plant^{-1} (Fig. 1F). This value was higher than the maximum cumulative soybean aphid-day plant^{-1} values attained with initial V5 infestation levels of 50 and 100 soybean aphids plant^{-1} (Fig. 1G–1H), which appeared to indicate that increasing initial soybean aphid infestation levels resulted in decreasing maximum cumulative soybean aphid-days plant^{-1} later in the season. The maximum cumulative soybean aphid-days plant^{-1} was 44 to 80% lower when

GDD(°C): 63 285 509 766 975

A. Aphids introduced at V5 ▲; Aphids introduced at R2 ●
$Y = [476.7][0.9875^{(X-218.8)^2}]$, $R^2 \approx 1.00$, (0)†
$Y = [147.7][0.9972^{(X-224.0)^2}]$, $R^2 = 0.83$

B. $Y = [21024][0.9889^{(X-231.1)^2}]$, $R^2 \approx 1.00$
$Y = [2932.6][0.9955^{(X-231.2)^2}]$, $R^2 \approx 1.00$, 10

C. $Y = [15429.7][0.9915^{(X-227.6)^2}]$, $R^2 = 0.99$
$Y = [2304.1][0.9985^{(X-242.2)^2}]$, $R^2 = 0.95$, 50

D. $Y = [10735.7][0.9919^{(X-230.9)^2}]$, $R^2 = 0.98$
$Y = [5861.5][0.9948^{(X-238.3)^2}]$, $R^2 \approx 1.00$, 100

E. Aphids introduced at V5 ▲; Aphids introduced at R2 ●
$Y = \dfrac{7901}{1+e^{[(48.9776)-(0.2237)(X)]}}$, $R^2 \approx 1.00$
$Y = \dfrac{4412}{1+e^{[(30.9529)-(0.1370)(X)]}}$, $R^2 = 0.99$, (0)†

F. $Y = \dfrac{384121}{1+e^{[(39.8802)-(0.1718)(X)]}}$, $R^2 \approx 1.00$
$Y = \dfrac{76718}{1+e^{[(33.0793)-(0.1427)(X)]}}$, $R^2 \approx 1.00$, 10

G. $Y = \dfrac{326596}{1+e^{[(31.3124)-(0.1375)(X)]}}$, $R^2 \approx 1.00$
$Y = \dfrac{76706}{1+e^{[(29.2561)-(0.1239)(X)]}}$, $R^2 \approx 1.00$, 50

H. $Y = \dfrac{246659}{1+e^{[(30.1249)-(0.1302)(X)]}}$, $R^2 \approx 1.00$
$Y = \dfrac{130913}{1+e^{[(40.0269)-(0.1693)(X)]}}$, $R^2 \approx 1.00$, 100

Soybean aphids plant^{-1}

Cumulative aphid-days plant^{-1}

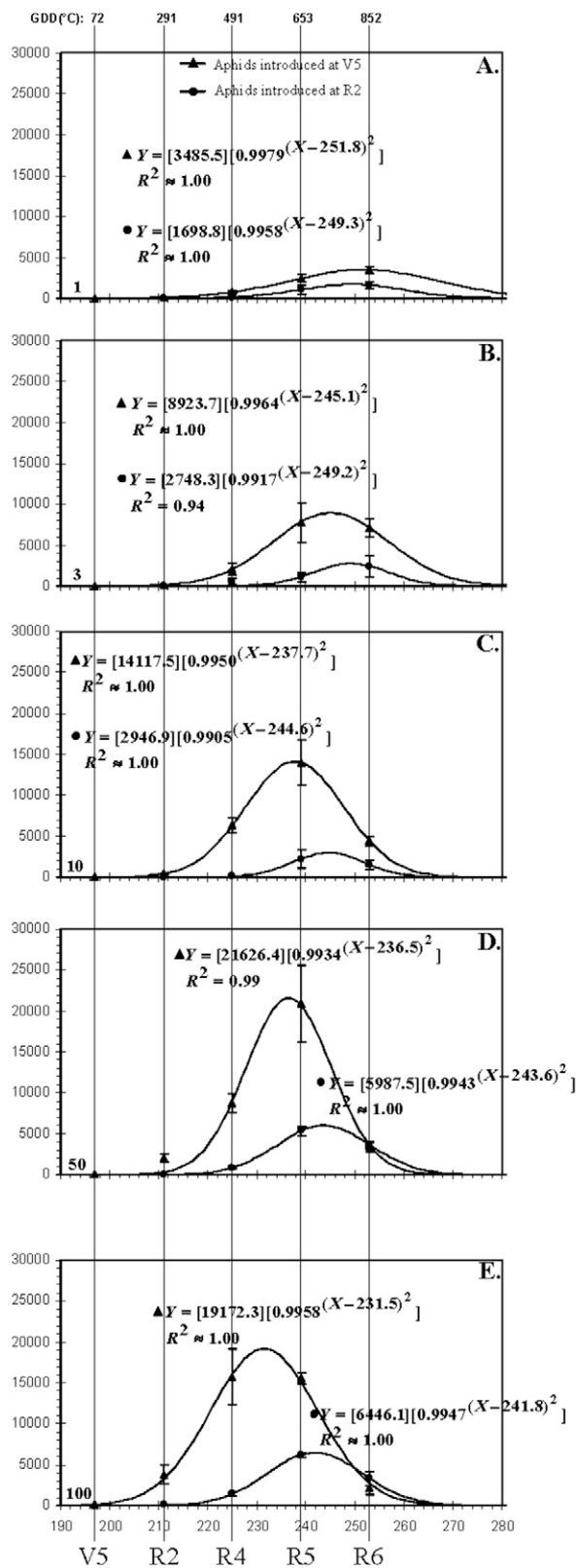V5 R2 R4 R5 R6

Day of year and plant growth stage

Fig. 1. Population dynamics of soybean aphids during the 2003 season (mean ± standard error). Numbers on the lower left corner of each graph are the initial number of soybean aphids introduced per plant. †Soybean aphids may have been accidentally introduced during initial cage set up.

soybean aphids were initially introduced 16 d later (DOY 204; 23 July), at R2 rather than at V5 (Fig. 1E–1H).
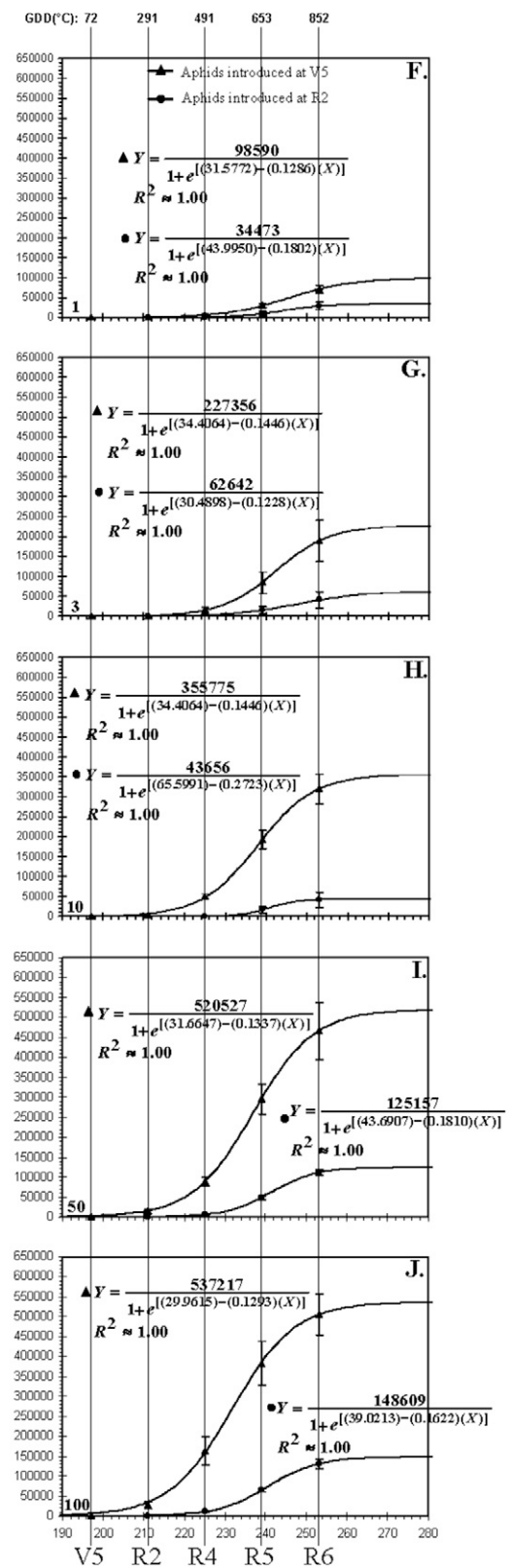
The time when the rate of soybean aphid-day accumulation was fastest was determined by calculating the inflection point of the logistic curve. Inflection point was calculated as the ratio of the B and C constants from the logistic formula (see Materials and Methods). For example, the inflection point of the logistic curve describing the cumulative soybean aphid-day plant^{-1} over time from an initial V5 infestation with 10 soybean aphids plant^{-1} occurred on DOY 232 (39.8802/0.1718)

corresponding to 20 Aug. 2003, when plants were at the R5 growth stage (Fig. 1F). Inflection points for V5 infestations with 50 and 100 soybean aphids plant^{-1} occurred on DOY 228 (16 August) and 231 (19 August), respectively, also at R5 growth stage (Fig. 1G–1H). Calculation of the inflection points for initial soybean aphid infestations at R2 revealed that the fastest accumulation of soybean aphid-days on the soybean plants also occurred at or near the R5 growth stage, at DOY 232–236. It took 43–44 d for the V5 infestations and 28–32 d for the R2 infestations to reach their inflection points.

Fig. 2. Population dynamics of soybean aphids during the 2004 season (mean ± standard error). Numbers on the lower left corner of each graph are the initial number of soybean aphids introduced per plant.

In 2004, initial soybean aphid infestations at V5 (DOY 194; 12 July) with 1, 3, 10, 50, and 100 soybean aphids plant^{-1} resulted in increasing maximum cumulative soybean aphid-days plant^{-1} that appeared to level off between 520,000 and 540,000 soybean aphid-days plant^{-1} (Fig. 2E–2J). The maximum cumulative soybean aphid-days plant^{-1} in the soybean

plants initially infested with soybean aphids at R2 (DOY 209; 27 July) were 65 to 88% lower than the maximum cumulative soybean aphid-days plant^{-1} for the V5-infested plants. The inflection points for the 1, 3, 10, 50, and 100 soybean aphids plant^{-1} applied at V5 occurred on DOY 246 (2 Sept.), 242 (29 August), 238 (25 August), 237 (24 August), and 232 (19 August), respectively. Inflection points were at 38 to 52 d after infestation regardless of starting soybean aphid population, and were consistently close to or at the R5 (beginning seed) growth stage (Fig. 2E to 2J). Inflection points of the cumulative soybean aphid-days plant^{-1} for the soybean aphid levels introduced to their host plants at R2 occurred on DOY 244, 248, 241, 241, and 241, respectively, 32 to 39 d after infestation, also at or near the R5 stage.

Some generalizations can be made from the above results. First, it appears that there is a limit to the maximum peak number of soybean aphids plant^{-1} and the maximum cumulative soybean aphid-days plant^{-1} that can be attained on the soybean plant. In this study, the maximum peak soybean aphid number attained was about 21,024 soybean aphids plant^{-1} in 2003, and 21,626 soybean aphids plant^{-1} in 2004. The highest initial infestations did not necessarily produce the highest peaks. In 2003, for example, the highest peak was on plants initially infested with 10 soybean aphids plant^{-1} at V5 (Fig. 1B); in 2004, it was on plants initially infested with 50 soybean aphids plant^{-1} at V5 (Fig. 2D). The maximum cumulative soybean aphid-days plant^{-1} attained were about 384,000 and 537,000 soybean aphid-days plant^{-1} in 2003 and 2004.

Most of the peak soybean aphid numbers and inflection points occurred at or close to the R5 soybean growth stage regardless of whether the soybean aphids were initially introduced to the plant hosts at V5 or R2. However, the lower initial infestation levels (1 and 3 soybean aphids plant^{-1}) peaked and reached inflection points noticeably later than the higher (10, 50, and 100 soybean aphids plant^{-1}) initial infestation levels. The peaks and inflection points of the latter initial infestation levels were similar (Fig. 1 and 2). The difference between the V5- and R2-initial infestations in terms of the DOY when peak numbers occurred was only 7 d. Averaged across initial infestation levels, peak soybean aphid numbers in the V5- and R2-infested soybean occurred on DOY 227 and 234 in 2003, and on DOY 238 and 245 in 2004. To reach peak numbers in 2003 and 2004, the soybean aphids took 39 and 47 d if introduced at V5, and 30 and 37 d if introduced at R2, respectively. When averaged across initial soybean aphid infestation levels, the inflection point or the time when the soybean aphids were multiplying the fastest also fell on the R5 soybean growth stage. In 2003, for example, the inflection point occurred on DOY 228 for V5-infested soybean and on DOY 223 for R2-infested plants, a difference of only 5 d even though the initial V5 and R2 infestations were 16 d apart. The same was observed in 2004 when the inflection points occurred on DOY 239 and 243 also at the R5 soybean growth stage.

The beginning seed stage (R5) appears to be the approximate stage when the soybean aphids both reach their peak numbers as well as their maximum rates of multiplication. In contrast, soybean aphid numbers and multiplication rates declined sharply when the soybean plants reached the R6 or green bean stage (Fig. 1 and 2). According to Ritchie et al. (1999),

several events occur midway between the R5 and R6 stages: (i) the plant attains its maximum height; (ii) nitrogen-fixation rates peak and begin to drop rapidly; and (iii) the seeds begin a period of rapid dry weight and nutrient accumulation. We hypothesize that these seasonal changes in the soybean plant, especially nitrogen-fixation and the mobilization of N-fixation products from vegetative organs to developing seeds, also influence the reproduction and population dynamics of the soybean aphids. It has been previously demonstrated that soybean aphid reproduction appears to be positively correlated with the N content of the host plant in soybean (Hu et al., 1992; Myers and Gratton, 2006). Reproduction in other aphid species is also correlated to N content in other host plant species (Nevo and Coll, 2001; Pettit et al., 1994).

The observed differences in peak soybean aphid numbers and reproductive rates when the soybean aphids were introduced at V5 or R2 could have been due to the fewer number of days that the soybean aphids were allowed to multiply on their host. Although the peak numbers and reproductive rates were lower for R2-introduced soybean aphids, the shapes of the bell-shaped and logistic curves were similar for the V5- and R2-introduced soybean aphids (Fig. 1 and 2). The maximum possible soybean aphid number that can be attained plant^{-1} appeared to be about 21,626 soybean aphids plant^{-1}. Maximum cumulative soybean aphid-days was 537,217 soybean aphid-days plant^{-1}.

According to Riedell et al. (2005) and Osborne and Riedell (2006), the concentration of N fixation products (e.g., ureides) by soybean shoots increases rapidly starting at R1, peaks at around R5, and dramatically drops to near 0 by R7. Thus, the symmetrical bell-shaped curves that described soybean aphid numbers over time (Fig. 1A–1D and 2A–2E), as well as the time of inflection in the logistic curves that describe the rate of soybean aphid multiplication over time (Fig. 1E–1H and 2E–2J) occurred in a manner similar to the previously described seasonal rise and fall of ureide-N in the soybean host plants. Taken together, these observations suggest that peak soybean aphid numbers and reproductive rates coincide with the highest levels of ureide-N in the host soybean plant. The above observations on the interrelationships among soybean aphid numbers, soybean plant development stage, and N fixation products may have important implications in managing soybean aphids to prevent soybean yield losses.

Soybean Yield Loss Due to Soybean Aphids

Soybean aphid feeding injury reduces the number of pods plant^{-1}, seeds pod^{-1}, and seed size (Beckendorf et al., 2008). In addition to reducing yield components, soybean aphid feeding can reduce the oil content of the harvested seeds (Riedell and Catangui, 2006). Defining a mathematical relationship between soybean aphid numbers during the growing season and eventual yield or yield loss would allow development and refinements of economic threshold recommendations for soybean aphid population management and yield loss prevention. In 2003, there was a strong mathematical relationship between soybean aphid numbers during a specific growth stage and the eventual yield at harvest (Fig. 3A–3C). There also was a strong relationship between increasing soybean aphid numbers and yield expressed as percentage of the maximum yield
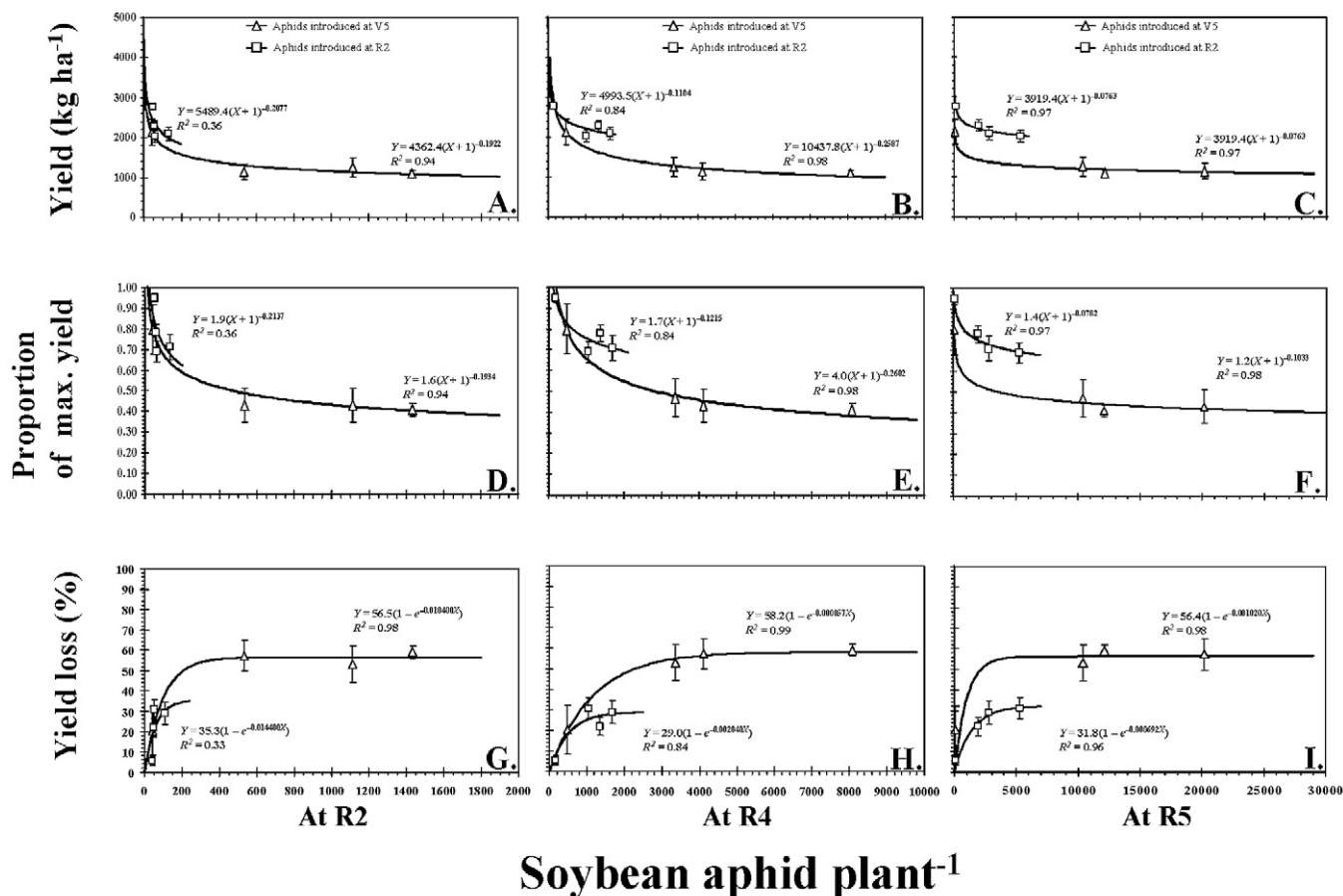
Fig. 3. Effect of soybean aphid numbers at R2, R4, and R5 on soybean seed yield during the 2003 season expressed as actual yield, yield as proportion of the maximum yield, and percentage yield loss (mean ± standard error).

(Fig. 3D–3F). The maximum yields recorded in the V5- and R2-infested soybean in 2003 were 2674 kg ha^{-1} and 2919 kg ha^{-1}. In 2004, the maximum yields recorded for the V5- and R2-infested soybean were 3667 and 3147 kg ha^{-1}. The power equation used appeared to fit the soybean aphid numbers (at specific growth stages) and yield data very well as indicated by the R^2 values of 0.94–0.97 in the V5- and 0.36–0.97 in the R2-infested soybean.

The decline in yield caused by soybean aphid feeding injury eventually leveled off so that no matter how high the soybean aphid numbers became, the soybean plants were still able to produce a minimum yield. In the V5-infested soybean in 2003, the soybean plants produced a minimum yield of 1000 kg ha^{-1} (about 38% of the maximum yield) despite being subjected to infestation levels as high as 21,000 soybean aphids plant^{-1} at R5 (Fig. 3A–3F). The mathematical relationship between soybean aphids plant^{-1} and percentage yield loss indicates a maximum possible yield loss of 57% during the 2003 season (Fig. 3G–3I). Yield decline due to increasing soybean aphid numbers in the R2-infested plants was less severe than for the V5-infested soybean (Fig. 3A–3I). Soybean aphids introduced at V5 had more time to multiply and reached higher peaks. Soybean aphid infestation at V5 inflicted more injury to the host plant than soybean aphids introduced at R2 (Beckendorf et al., 2008). In the present study, the highest soybean aphid population reached on the R2-infested plants in 2003 was about 6000 soybean aphids plant^{-1}. Minimum yield was about 2000 kg ha^{-1} or about 66%

of the maximum yield. The maximum possible yield loss due to increasing soybean aphid number was 32%.

In 2004, the highest soybean aphid number reached on the V5-infested soybean was also about 21,000 soybean aphids plant^{-1} (Fig. 4A–4I). The minimum yield produced was about 1200 kg ha^{-1} or 30% of the maximum yield. Maximum possible yield reduction in 2004 was 86%. In the R2-infested soybean plants, the highest soybean aphid population reached was about 6000 soybean aphids plant^{-1} and the minimum yield produced was about 1900 kg ha^{-1} or 62% of the maximum yield. The maximum possible reduction in yield due to soybean aphids in 2004 for the R2-infested soybean was 51%. Thus, although the soybean plant host was severely injured by the soybean aphids, the yield loss was not total. We hypothesize that the ability of soybean plants to produce some yield no matter how high the soybean aphid numbers may have been due to compensatory growth after the R5 stage when the soybean aphids plant^{-1} started to decline dramatically (Fig. 1 and 2). We speculate that the transient nature of soybean aphid infestation may have allowed the soybean plants to compensate for soybean aphid injuries between the time when the soybean aphid populations decreased (R5) and the mature seed stage. Although other factors may contribute to this, compensation to foliar insect injury can occur by compensatory growth and delayed leaf senescence (Higley, 1992). Indeterminate cultivars, such as the one used in this study (Gebhardt et al., 1999), have excellent potential for compensatory growth after
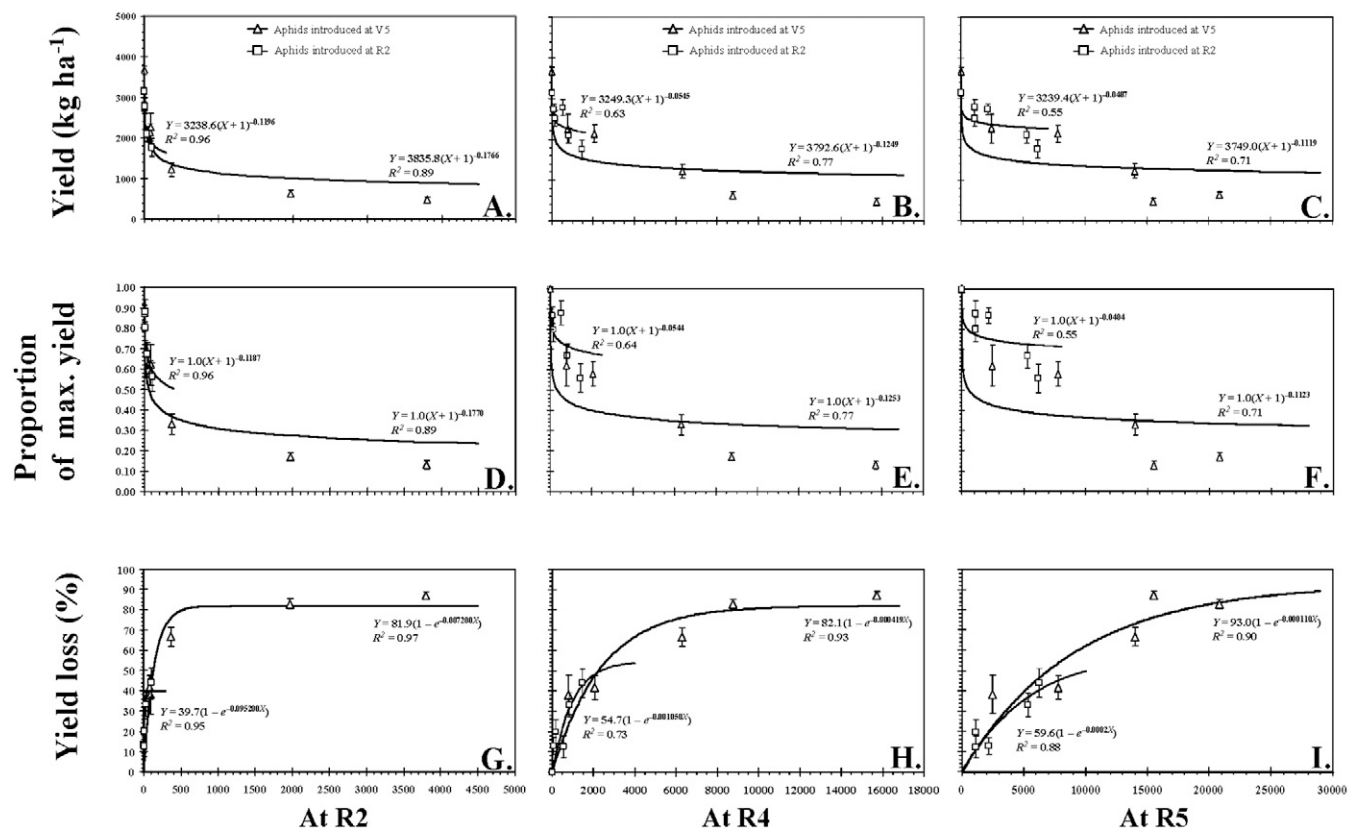
Fig. 4. Effects of soybean aphid numbers at R2, R4, and R5 on soybean seed yield during the 2004 season expressed as actual yield, yield as proportion of the maximum yield, and percentage yield loss (mean ± standard error).

insect injury (Haile et al., 1998). The physiological basis of this observed theoretical maximum possible yield reduction is not fully understood, and additional research is needed on soybean stress-response mechanisms to soybean aphid feeding injury.

Development of Stage-Specific Economic Injury Levels

The combined 2003–2004 data suggest that, on average, the maximum possible yield losses due to soybean aphids were 75% for plants infested at V5 and 48% at R2 (Fig. 5A–5F and 6A–6F). There was a maximum possible reduction in yield regardless of the numbers of soybean aphids during the growing season. This leveling off or diminishing return of yield loss due to increasing soybean aphid numbers was the basis of using the Mitscherlich law or "the law of the diminishing increment" model (Spillman, 1924). An inherent feature of this model is that the initial number of soybean aphids on the soybean plant has more impact on yield than each additional soybean aphid thereafter, until the contribution of the latter soybean aphids becomes negligible (maximum possible yield loss or maximum possible reduction in yield) (Fig. 5A–5F and 6A–6F).

The regression equations for calculating the stage-specific (for R2, R4, and R5) EILs for soybean aphid infestations starting at V5 are as follows (Fig. 5A–5C):

$$\text{EIL}_{V5@R2} = \{\ln[1 - (GTP/68.1\%)]\} /-0.009840\% \text{ soybean aphid}^{-1} \text{ plant}^{-1} \qquad [1]$$

$$\text{EIL}_{V5@R4} = \{\ln[1 - (GTP/76.2\%)]\} /-0.000411\% \text{ soybean aphid}^{-1} \text{ plant}^{-1} \qquad [2]$$

$$\text{EIL}_{V5@R5} = \{\ln[1 - (GTP/77.0\%)]\} /-0.000143\% \text{ soybean aphid}^{-1} \text{ plant}^{-1} \qquad [3]$$

The regression equations for calculating the stage-specific (for R2, R4, and R5) EILs for soybean aphid infestations starting at R2 are as follows (Fig. 5D–5F):

$$\text{EIL}_{R2@R2} = \{\ln[1 - (GTP/27.4\%)]\} /-0.167200\% \text{ soybean aphid}^{-1} \text{ plant}^{-1} \qquad [4]$$

$$\text{EIL}_{R2@R4} = \{\ln[1 - (GTP/32.5\%)]\} /-0.002480\% \text{ soybean aphid}^{-1} \text{ plant}^{-1} \qquad [5]$$

$$\text{EIL}_{R2@R5} = \{\ln[1 - (GTP/44.3\%)]\} /-0.000309\% \text{ soybean aphid}^{-1} \text{ plant}^{-1} \qquad [6]$$

For calculating stage-specific cumulative soybean aphid-day EILs (ADEILs), the regression equations are as follows (Fig. 6A–6F):

$$\text{ADEIL}_{V5@R2} = \{\ln[1 - (GTP/68.2\%)]\} /-0.001340\% \text{ soybean aphid-day}^{-1} \text{ plant}^{-1} \qquad [7]$$
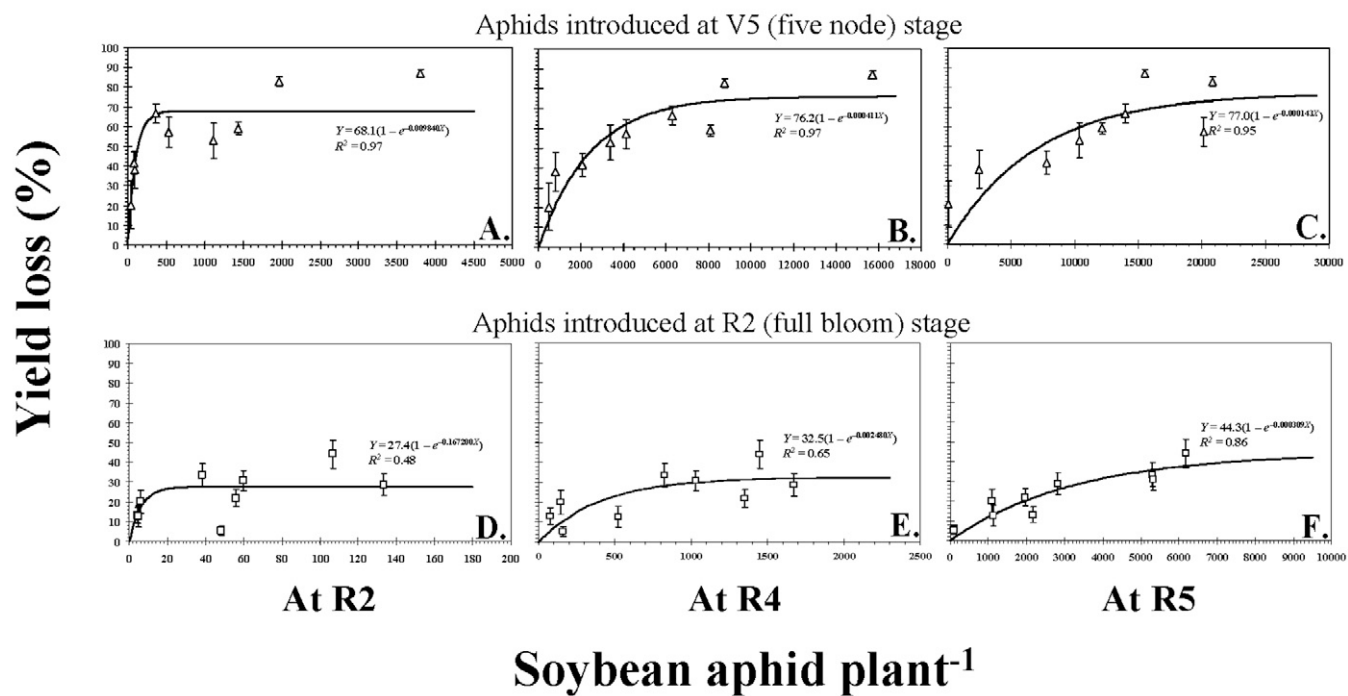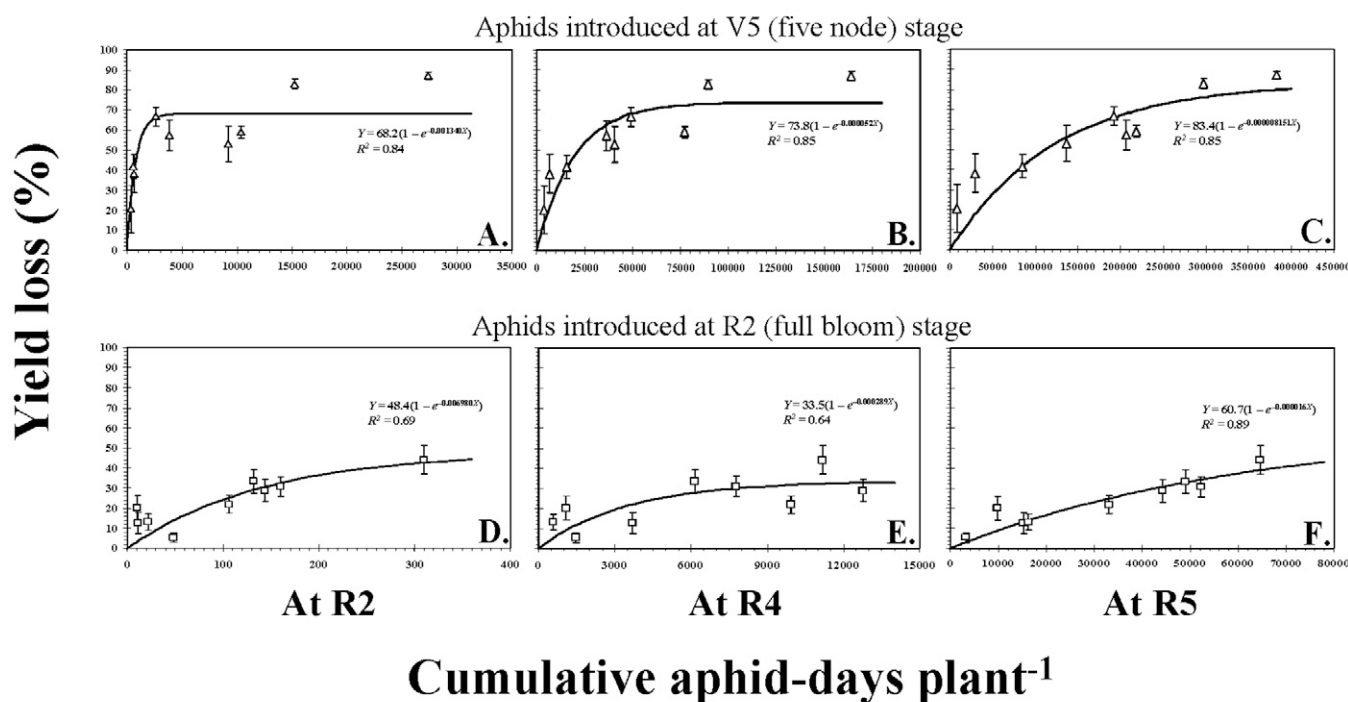
Fig. 5. Combined (2003 and 2004) effects of soybean aphid numbers at R2, R4, and R5 on soybean yield loss (mean ± standard error).

$\text{ADEIL}_{V5@R4} = \{\ln[1 - (\text{GTP}/73.8\%)]\}$

$/-0.000052\%$ soybean aphid-day^{-1} plant^{-1} [8]

$\text{ADEIL}_{R2@R2} = \{\ln[1 - (\text{GTP}/48.4\%)]\}$

$/-0.006980\%$ soybean aphid-day^{-1} plant^{-1} [10]

$\text{ADEIL}_{V5@R5} = \{\ln[1 - (\text{GTP}/83.4\%)]\}$

$/-0.000008151\%$ soybean aphid-day^{-1} plant^{-1} [9]

$\text{ADEIL}_{R2@R4} = \{\ln[1 - (\text{GTP}/33.5\%)]\}$

$/-0.000289\%$ soybean aphid-day^{-1} plant^{-1} [11]

Fig. 6. Combined (2003 and 2004) effects of cumulative soybean aphid-day accumulations at R2, R4, and R5 on soybean yield loss (mean ± standard error).

$$\text{ADEIL}_{\text{R2@R5}} = \{\ln[1 - (\text{GTP}/60.7\%)]\}$$
$$/{-}0.000016\% \text{ soybean aphid-day}^{-1} \text{ plant}^{-1} \qquad [12]$$

Example

A soybean grower from the north-central United States plans to treat for soybean aphids during the 2010 growing season using an insecticide applied by a fixed-wing aircraft. The grower's soybean field had been yielding 3700 kg ha^{-1}. Combined insecticide plus application cost is \$24.71 ha^{-1} and the soybean market value is \$0.29 kg^{-1}. What are the stage-specific EILs (in EIL and ADEIL) of the soybean aphid at R2, R4, and R5 if the soybean aphids were first detected infesting the field at V5? (i) GT = control cost/market value = \$24.71/ha/\$0.29/kg = 85.21 kg ha^{-1}; (ii) GTP = (GT/yield potential)(100) = 2.30%. The GTP is the GT expressed as a proportion of the yield potential of the field.

$$\text{EIL}_{\text{V5@R2}} = \{\ln[1 - (2.30\%/68.1\%)]\}$$
$$/{-}0.009840\% \text{ soybean aphid}^{-1} \text{ plant}^{-1}$$
$$= 3.5 \text{ soybean aphids plant}^{-1} \qquad [3.1]$$

$$\text{EIL}_{\text{V5@R4}} = \{\ln[1 - (2.30\%/76.2\%)]\}$$
$$/{-}0.000411\% \text{ soybean aphid}^{-1} \text{ plant}^{-1}$$
$$= 74.6 \text{ soybean aphids plant}^{-1} \qquad [3.2]$$

$$\text{EIL}_{\text{V5@R5}} = \{\ln[1 - (2.30\%/77.0\%)]\}$$
$$/{-}0.000143\% \text{ soybean aphid}^{-1} \text{ plant}^{-1}$$
$$= 212.1 \text{ soybean aphids plant}^{-1} \qquad [3.3]$$

$$\text{ADEIL}_{\text{V5@R2}} = \{\ln[1 - (2.30\%/68.2\%)]\}$$
$$/{-}0.001340\% \text{ soybean aphid-day}^{-1} \text{ plant}^{-1}$$
$$= 25.6 \text{ soybean aphid-days plant}^{-1} \qquad [3.7]$$

$$\text{ADEIL}_{\text{V5@R4}} = \{\ln[1 - (2.30\%/73.8\%)]\}$$
$$/{-}0.000052\% \text{ soybean aphid-day}^{-1} \text{ plant}^{-1}$$
$$= 608.9 \text{ soybean aphid-days plant}^{-1} \qquad [3.8]$$

$$\text{ADEIL}_{\text{V5@R5}} = \{\ln[1 - (2.30\%/83.4\%)]\}$$
$$/{-}0.000008151\% \text{ soybean aphid-day}^{-1} \text{ plant}^{-1}$$
$$= 3430.9 \text{ soybean aphid-days plant}^{-1} \qquad [3.9]$$

Thus, for soybean aphid infestations starting at V5, the stage-specific EILs for a soybean field with a yield potential of 3700 kg ha^{-1}, a soybean market value of \$0.29 kg^{-1}, and a control cost of \$24.71 ha^{-1} are 3.5, 74.6, and 212.1 soybean aphids plant^{-1} at R2, R4, and R5, respectively. The stage-specific EILs in cumulative aphid-days plant^{-1} are 25.6, 608.9, and 3430.9 soybean aphid-days plant^{-1}.

The stage-specific EIL and ADEIL calculated above were plotted and fitted with a symmetrical bell-shaped and logistic curve, respectively (Fig. 7). Any observed soybean aphid number or aphid-day accumulation on the field exceeding the calculated EIL or ADEIL at any given time from R2 to R5 should be controlled to prevent soybean yield loss. Scouting for the soybean aphids can be focused on or several days before the critical reproductive stages of soybean. In general, the soybean plant is tolerant of stress during the vegetative stages but is sensitive to it during the reproductive stages (Ritchie et al., 1999). The approximately 42-d duration from V5 through R5 is the logical time to manage for the soybean aphid (Fig. 7).

The different phases of the logistic curve should be used to guide field activities. That is, the predicted time of occurrence of the lag phase, the inflection point, and the log phase can be used as action thresholds on or before which control treatments must be applied to optimize soybean aphid population control. Scouting efforts must also be conducted based on the information provided by the logistic curve in relation with the observed plant development stages. Because the rate of increase of a soybean aphid population is highest at the inflection point, insecticidal sprays, for example, may produce better aphid control if applied before the inflection point or perhaps even during the lag phase when soybean aphids are multiplying the slowest. Also, application of insecticides with low efficacy and little residual action (e.g., organic insecticides) should be made early in the lag phase to take advantage of the slowest rate of increase of the soybean aphid population.

In the above example, the inflection point occurred on DOY 233 (20 August) at 2083 cumulative soybean aphid-days plant^{-1} or 168 soybean aphids plant^{-1} (Fig. 7). The end of the lag phase occurred on DOY 224 (11 August) and the end of the logarithmic growth phase occurred on DOY 241 (28 August). The field can be scouted starting at V5 to establish initial infestation, and scouted regularly at any time between the approximate 28-d duration from R2 (DOY 211; 29 July) through R5 (DOY 239; 26 August). Insecticidal sprays must be applied immediately if the stage-specific EIL or ADEIL are exceeded, ideally, before the inflection point is reached on 20 August. The R5 stage appears to be the last soybean development stage that can be treated for soybean aphids because aphid numbers may peak at this stage then dramatically decline thereafter (Fig. 1, 2, and 7). However, control treatments at R5 may be less than ideal because R5 may be past the inflection point of the soybean aphid-day logistic curve, and in fact may be close to the end of the log growth phase of the aphids. Calculation of EIL and ADEIL, and timing of control applications must be adjusted if the initial aphid infestation occurred at R2 instead of V5 as discussed above. The more conservative procedures for V5 initial aphid infestation may be used if the time of initial aphid infestation was not known.

Future field research is needed to confirm the applicability of the above recommendations for the diverse soybean growing conditions of the United States and the various interactions among soybean cultivars, soybean market value, soybean aphid control cost and efficacy, soil fertility and moisture, yield potential of the field, and other variables unforeseen by the authors of this current study.

CONCLUSIONS

The relationship between DOY and soybean aphids plant^{-1} was described by fitting an equation for a symmetrical bell-shaped curve. This enabled accurate calculations for the peak number of soybean aphids plant^{-1}, the time of peak soybean aphid occurrence, and the number of days it took for the soybean aphids to reach their peak numbers. The rate of soybean
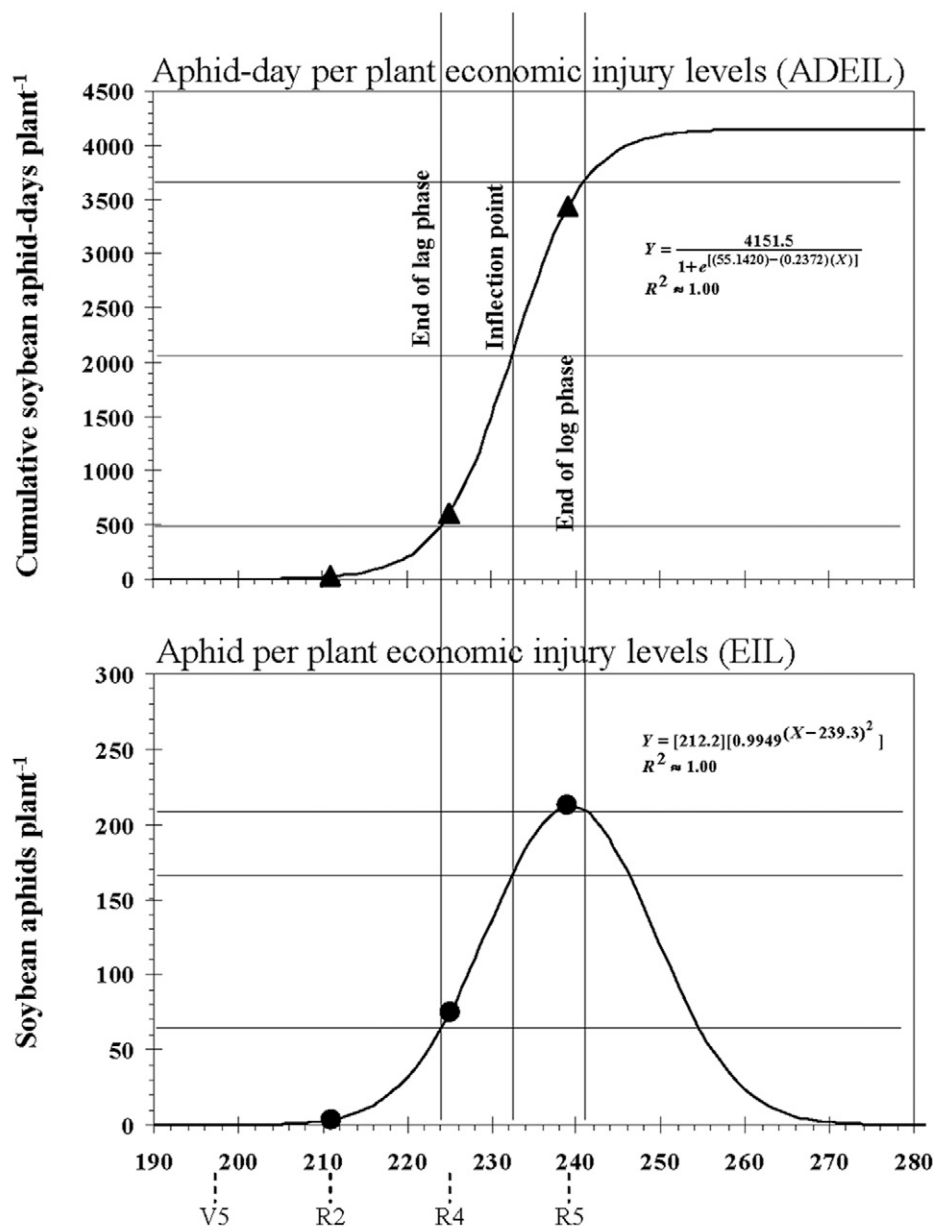
Fig. 7. Graphical representation of the calculated stage-specific EIL fitted with a symmetrical bell-shaped curve, and the ADEIL fitted with a logistic curve showing the DOY when the inflection point, lag phase, and log phase occurred.

aphid multiplication over time on the soybean plants was also measured by fitting a logistic growth curve on the DOY-cumulative soybean aphid-day plant^{-1} data. The logistic curve enabled calculation for the inflection point (the time when the soybean aphids were multiplying the fastest) and calculation of the maximum possible cumulative soybean aphid-days plant^{-1}, which is the maximum infestation severity inflicted by the soybean aphids on the soybean plant. The R5 (beginning seed) soybean development stage was the approximate time when the soybean aphids reached their peak numbers and maximum rates of multiplication. We speculate that this could be due to the seasonal rise and fall of ureide-N in the soybean host plants. Maximum soybean aphid reproduction, at R5, may coincide

with peak ureide-N level on the host at this soybean development stage. Soybean aphids introduced to the soybean plants at V5 reached much higher peak numbers and maximum cumulative soybean aphid-days than soybean aphids introduced at R2. Soybean aphids introduced at V5 also inflicted more injury and yield loss to the host plants than soybean aphids introduced at R2.

There were strong mathematical relationships between soybean aphid infestations at R2, R4, and R5 and percentage yield loss at harvest. However, there appeared to be an upper limit or maximum possible yield loss that was inflicted by the soybean aphids to the soybean plants. The maximum possible yield losses due to soybean aphids was 75% for infestations starting at V5, and 48% for infestations starting at R2. The

Mitscherlich law or "the law of the diminishing increment" model was used to describe the quantitative relationships between soybean aphid numbers at R2, R4, and R5 and percentage yield loss at harvest. The resulting regression equations were then used to calculate stage-specific EILs of the soybean aphids on soybean.

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